

Mandibular Ramus Flexure: A New Morphologic Indicator of Sexual Dimorphism in the Human Skeleton

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ABSTRACT In the skeleton, male and female characteristics lie along a continuum of morphologic configurations and metric values. Size alone is not the best indicator of sex. In contrast, morphologic differences that arise from genetically sex-linked growth and development allow better separation of the sexes. This study presents a new morphologic indicator of sexual dimorphism in the human mandible. A sample of 300 mandibles from adults of known sex primarily from the Dart collection was analyzed. Of these, 100 were found to have obvious bony pathologies and/or excessive tooth loss ("pathologic" sample). Thus, the normative sample consisted of 200 individuals (116 males, 84 females). Examination of morphologic features led to the discovery of a distinct angulation of the posterior border of the mandibular ramus at the level of the occlusal surface of the molars in adult males. Flexure appears to be a male developmental trait because it is only manifest consistently after adolescence. In most females, the posterior border of the ramus retained the straight juvenile shape. If flexure was noted, it was found to occur either at a higher point near the neck of the condyle or lower in association with gonial prominence or eversion. In the normative sample, overall prediction accuracy from ramus shape was 99%. When the "pathologic" sample was analyzed separately, 91.0% were correctly diagnosed. Because the African samples were overwhelmingly black, this trait was also tested on American samples (N = 247) of whites (N = 85), Amerinds (N = 66), and blacks (N = 96) that included a mix of healthy individuals and those with extensive tooth loss and evidence of pathology. The results were nearly identical to those of the "pathologic" African sample, with accuracies ranging from about 91% in whites and blacks to over 92% in Amerinds. Total accuracy for all African and American samples combined (N = 547) is 94.2%. In conclusion, at 99%, sexing from the shape of the ramus of a healthy mandible is on a par with accuracy attainable from a complete pelvis. Moreover, there is no record that any other single morphologic or metric indicator of sex (that has been quantified from the adult skeleton) surpasses the overall accuracy attained from the more representative mixed sample produced by combining all groups assessed in this study. The usefulness of this trait is enhanced by the survivability of the mandible and the fact that preliminary investigations show that the trait is clearly evident in fossil hominids. © 1996 Wiley-Liss, Inc.

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In the skeleton, male and female characteristics run through a continuum of morphologic configurations and metric values. A true understanding of the nature of human sexual dimorphism and the many factors that affect its expression is fundamental to and inexorably linked with the study of human growth, development, and evolution. Isolating, interpreting, and quantifying the manifestations of sex is an essential part of all skeletal analyses. Moreover, distinguishing sex differences from evolutionary modifications in hominid fossils is of prime phylogenetic importance.

The focus on osteometric approaches, such as discriminant function analysis, has made it clear that size alone is not the best indicator of sex (see Stewart, 1954, Birkby, 1966; Kimura, 1982; Krogman and İşcan, 1986; St. Hoyme and İşcan, 1989; Novotny et al., 1993). In addition, size-based methods are extremely population-specific. In contrast, morphologic differences which arise from genetically controlled, sex-linked patterns of growth and development are likely to allow more reliable separation of the sexes because they reflect inherent rather than highly variable functional and environmental factors (Borovansky, 1936; Stewart, 1954, 1979; Krogman and İşcan, 1986; St. Hoyme and İşcan, 1989; Novotný et al., 1993).

Sex differences have been investigated in nearly every part of the skeleton of human and non-human primates (see Brace, 1973; Frayer and Wolpoff, 1985; Ghesquiere et al., 1985; Krogman and İşcan, 1986; St. Hoyme and İşcan, 1989; Wood et al., 1991). Krogman and İşcan (1986) summarized adult sexing accuracy (both metrically and morphologically) from isolated bones: the complete pelvis (95%) and skull alone (90%), as well as combinations of bones: skull plus pelvis (98%), long bones plus pelvis (95%), long bones plus skull (90–95%), and long bones alone (80–90%).

Three basic criteria should guide the choice of skeletal elements that may be useful indicators of sex: 1) their morphology should clearly reflect anatomic and/or physiologic sex differences, 2) they should be able to withstand the rigors of skeletonization and fossilization, and 3) ideally the trait

should be recognizable through time and across paleospecies. At 95% accuracy, the complete pelvis is the most reliable site for sex determination in normal adults, yet it is rarely recovered intact from prehistoric burials and fossil sites. Therefore, since one does not always have the bone of choice in satisfactory condition, it is necessary to be able to maximize sex determination from as many bones as possible. The mandible is one of the most durable bones and is often one of the only remnants of rare fossil hominids.

In the mandible, growth is directed and morphology molded by numerous influences (see McNamara, 1975; Jacobsen, 1990). The developing deciduous dentition is known to differ in size and form between the sexes (e.g., Garn et al., 1964; Garcia-Godoy et al., 1985). From the prenatal period, statistically significant sex differences have been reported in both the muscles of mastication and mandibular dimensions (Malinowski, 1971). Moreover, it has been demonstrated that many factors involved in the formation of the mandible can be traced to its muscle attachments (Rickets, 1975; Weijs and Hillen, 1986), and dimorphism in the development of this musculature widens the male/female gap in ramus size and configuration until it reaches its full expression in adulthood (Strzalko, 1970). Sex-based variation in growth rates and patterns is also reflected in the mandible (Bogin, 1988). Mandibular growth begins in the chin region and continues at the condyles through and even beyond adolescence. Hunter and Garn (1972) found that, metrically, sexual dimorphism is localized in the ramus. They determined that the ramus was 14% longer in males than in females compared to only an 8% differential in all other facial dimensions. This was linked to continuing postpubertal mandibular bone growth in males (Walker and Kowalski, 1972). The full effects are not apparent by age 17, but are expressed beginning in the 3rd decade of life. There is ample evidence that the mandible is shaped in response to hormonal influences and both directly and indirectly by the muscle development thus stimulated (e.g., Petrovic et al., 1975; Rickets, 1975). Therefore, the high level of dimorphism in the ramus may arise in response to sex-specific hormones (or levels

of them) by receptors in susceptible skeletal sites.

There have been many publications dealing with sexual dimorphism in the metric and morphological traits of this bone (cf. Acsádi and Nemeskéri, 1970; Birkby, 1966; Krogman and İşcan, 1986; Sjøvold, 1988; St. Hoyme and İşcan, 1989; Novotný et al., 1993); however, no characteristic, singly or in combination, has approached the consistent reliability obtainable from a complete pelvis. There are only two reports of sexing accuracy from the mandible alone and both used discriminant functions: 1) Hanihara (1959) achieved about 85% correct classification from four dimensions; 2) Giles (1964), who averaged 84% from eight measurements, and 3) İşcan and Ding (1995) who reported 75% from 5 dimensions. Others have described and compared sex differences in the mandible but did not calculate prediction accuracies. De Villiers (1968) compared the means of a series of standard male and female craniofacial and mandibular dimensions and shape indices and determined that sexual dimorphism in South African black adults was significantly higher (t-test: $P < 0.01$) in the mandible. She also found the ramus significantly more dimorphic than the body of the mandible. Acsádi and Nemeskéri (1970) described apparently dimorphic traits in this bone, but did not quantify the effectiveness of individual morphological traits.

As part of a larger study of sexual dimorphism in the mandible and its underlying causes (Loth, 1996), the authors found that a heretofore undescribed trait—posterior ramus flexure—is a single, easily observable morphologic characteristic that rivals the complete pelvis in its effectiveness as an indicator of sex. The aim of this paper is to describe this new trait, explain its development, calculate its prediction accuracy in modern humans, and elaborate factors affecting its expression. Its applicability to fossil hominids is also discussed.

MATERIALS AND METHODS

The base sample consisted of 300 mandibles (175 males, 125 females) from individuals of known sex, age 20 and older. All but

five specimens (from the University of Pretoria Anatomy Department) were curated at the Dart collection in the Department of Anatomy and Human Biology, University of the Witwatersrand Medical School. Only nine were white; the rest were black, predominantly of South African origin. No completely edentulous specimens were included. Careful examination of the sample revealed that 100 individuals had obvious bony pathologies and/or excessive tooth loss (more than two posterior teeth missing antemortem). These mandibles were considered the "pathologic" sample (all 9 whites fell into this category). Thus the normative sample consisted of 200 African blacks (116 males, 84 females).

The morphological features of male and female mandibles were studied and compared. This led to the discovery of a distinct angulation of the posterior border of the mandibular ramus at the level of the occlusal surface of the molars in adult males (Figs. 1 and 2). In most females, the posterior border of the ramus was straight (Fig. 3) or, if flexure was observed, it was found to occur at a higher point near the neck of the condyle (Fig. 4). In most cases the shape is readily visible in norma lateralis, but assessment is improved by slowly rotating the posterior border of the ramus away from the observer. In a male, the flexure will be enhanced. In females, turning the mandible will either bring a clearly straight ramus into view or reveal that a change in direction occurs either higher, at the neck of the condyle (Fig. 4), or below the level of the teeth in cases with gonial prominence or eversion (Figs. 5A,B). It is also important not to confuse a strongly but gradually arched or curved upper ramus and condylar neck, as in Figure 5A, with the distinct angulation of true ramus flexure at the level of the occlusal surface of the molars (Figs. 1 and 2).

To conduct a systematic evaluation, a technician was asked to arrange the mandibles by accession number (which is independent of sex). Then the right and left ramus of each mandible was assessed separately by SRL. A score of +1 was assigned if flexure was present, -1 for a straight border (or flexure near the condyle or below the occlusal surface), and 0 if the shape was neither clearly

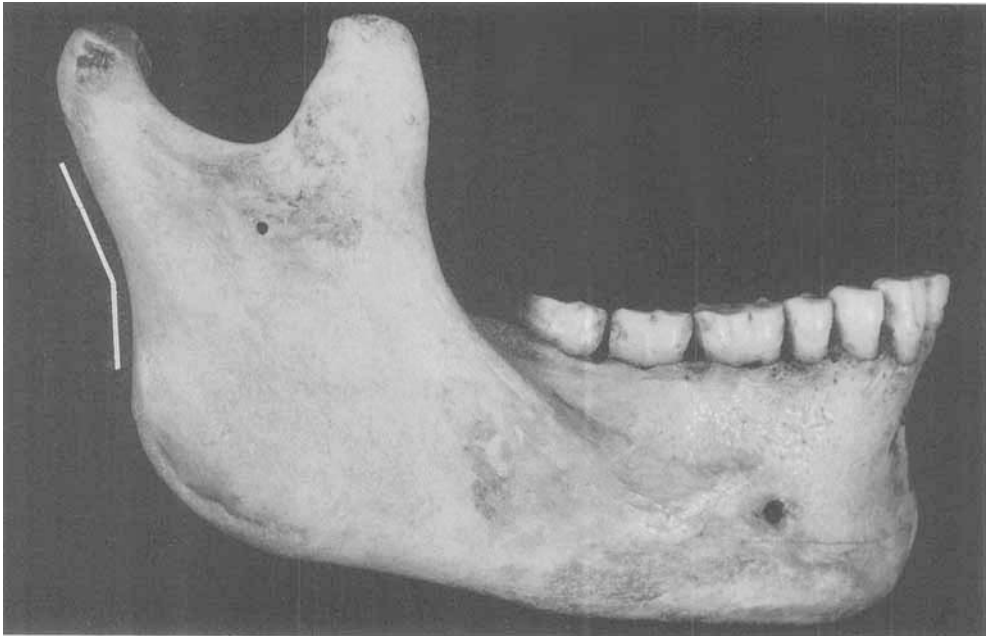


Fig. 1. Adult male mandible. Note the distinct angulation or flexure of the posterior border of the mandibular ramus at the level of the occlusal surface of the molars (photo by M. Henneberg).

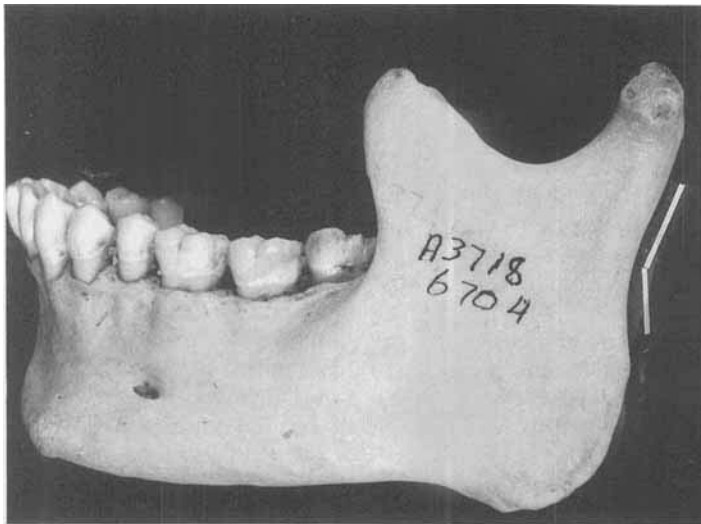


Fig. 2. Flexure of the posterior border of the mandibular ramus at the level of the occlusal surface of the molars is clear in this adult male mandible with gonial eversion and a very vertical ramus (photo by M. Henneberg).

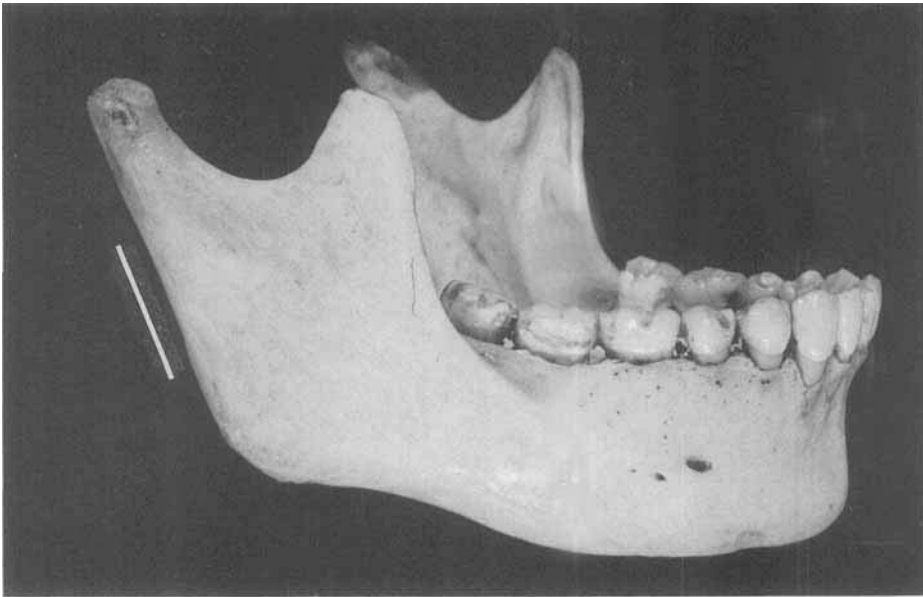


Fig. 3. This adult female mandible exhibits the straight posterior border of the ramus characteristic of adult females and juveniles of both sexes (photo by M. Henneberg).



Fig. 4. Adult female mandible with flexure at the neck of the condyle (arrow) well above the level of the occlusal surface of the molars (photo by M. Henneberg).

flexed nor straight. The scores for both rami were then added to yield a total of +2, +1, 0, -1, -2. The scores were then compared with the actual sex as recorded by the de-

partment of anatomy and prediction accuracies were calculated. Misclassified mandibles were re-examined to determine what underlying conditions may be responsible for

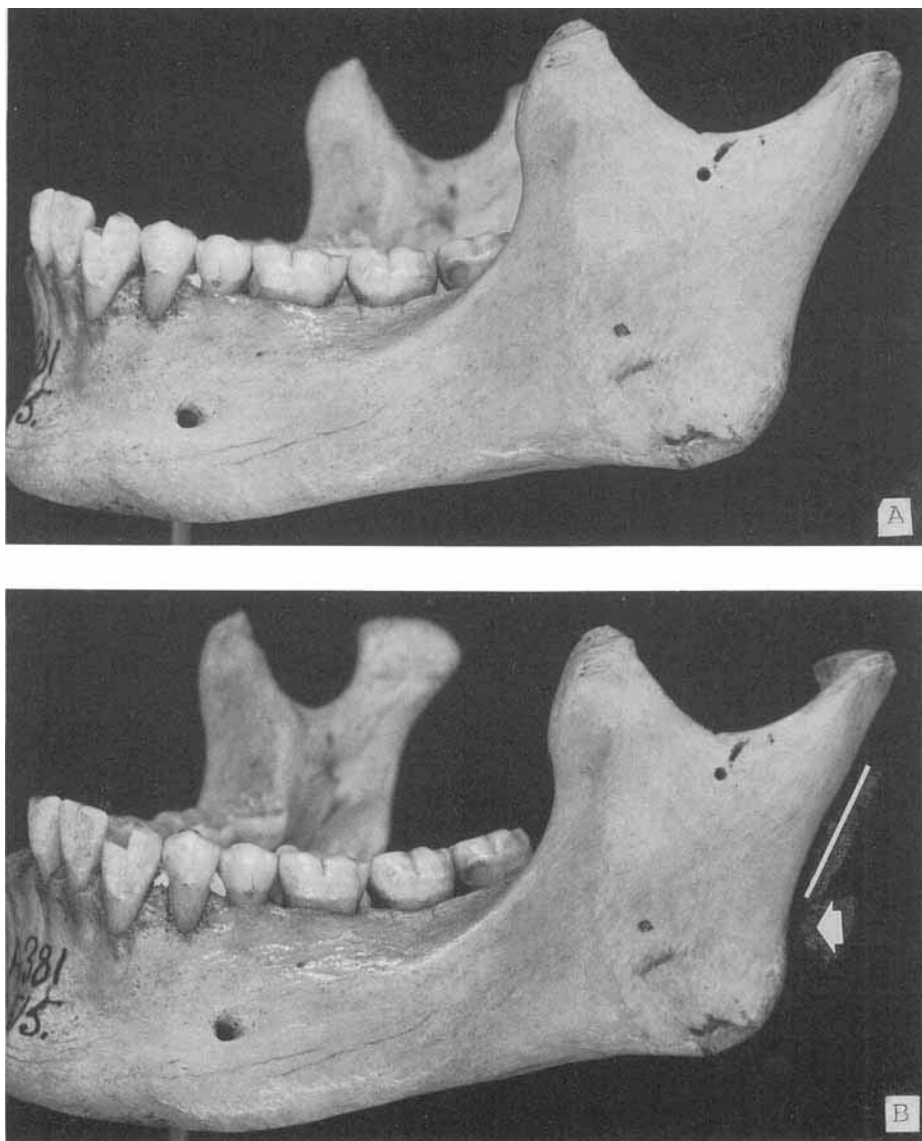


Fig. 5. In norma lateralis, the shape of this female mandible (A) is not easily assessed. Angulation produced by pronounced gonial eversion and gradually arching ramus should not be confused with flexure. Rotating the ramus of this same mandible (B) away from the observer clearly reveals that the posterior margin is straight at the occlusal surface of the molars, and any semblance of flexure is well below the occlusal plane at the upper limit of the everted gonial region (arrow) (photo by M. Henneberg).

deviations from the expected morphological configurations.

Because the African samples were almost exclusively black, this trait was then blind tested on 247 whites, Amerinds, and blacks. The European and American whites

(N = 85), Amerinds (N = 66), and blacks (N = 96) are housed at the Smithsonian Institution National Museum of Natural History in Washington, DC, and included a mix of healthy individuals and those with extensive tooth loss and evidence of pathology

TABLE 1. *Distribution of ramus shape scores by sex in the normative African black sample¹*

| Score | Males | Females | Total |
|-------|-------|---------|-------|
| +2 | 94 | 1 | 95 |
| +1 | 15 | 0 | 15 |
| 0 | 6 | 0 | 6 |
| -1 | 1 | 17 | 18 |
| -2 | 0 | 66 | 66 |
| Total | 116 | 84 | 200 |

¹ +2 = both rami flexed, +1 = one ramus flexed the other indeterminate, 0 = either both rami indeterminate or one flexed and the other straight, -1 = one ramus straight the other indeterminate, -2 = both rami straight.

(that did not result in extreme deformations). Nearly all whites and blacks are from the Terry collection of known, documented skeletons from the turn of the 20th century (Trotter, 1981). The white samples consisted of both American and European born individuals. Six other whites were known individuals who died of tuberculosis and whose bones were sent to Hrdlicka from Germany. Terry collection specimens were first selected on the basis of minimum age (20 years) and dental records. The final samples consisted of those with the most teeth (at least 2 posterior teeth present) and no seriously disfiguring conditions. The Amerinds consisted of adult archaeologic specimens with complete skeletons that had been previously assessed for sex from the pelvis. These mandibles were chosen based on completeness, preservation, presence of accompanying postcranial remains for verification of sex and age, and lack of severely disfiguring conditions.

All tests of significance were conducted by either calculating random error to build confidence intervals of percentage frequencies or Chi-squared tests in 2 × 2 contingency tables.

RESULTS

As can be seen in Table 1, most male mandibles in the normative sample (81%) were scored +2 indicating bilateral flexure. Similarly most females were scored -2 (79%), and all but one of the remaining females had a negative score (-1). Of the rest of the males, all but one were scored +1 or 0. Since no females received a 0, this score was considered to indicate a male. Therefore, to calculate overall accuracy, individuals with

TABLE 2. *Overall accuracy of ramus shape as an indicator of sex in normative African blacks¹*

| Sex | N | Ramus shape scores | | | | Accuracy by sex (%) |
|---------|-----|--------------------|-------|-------------|-------|---------------------------|
| | | -1 & -2 | | 0, +1, & +2 | | |
| | | N | % | N | % | |
| Males | 116 | 1 | 1.2 | 115 | 99.1 | 99.1 |
| Females | 84 | 83 | 98.8 | 1 | 0.9 | 98.8 |
| Total | 200 | 84 | 100.0 | 116 | 100.0 | 99.0 |

¹ Ramus shape scores of 0, +1, and +2 were deemed male; -1 and -2, female.

TABLE 3. *Distribution of ramus shape scores by sex in the pathologic African sample*

| Score | Males | Females | Total |
|-------|-------|---------|-------|
| +2 | 48 | 4 | 52 |
| +1 | 3 | 0 | 3 |
| 0 | 4 | 0 | 4 |
| -1 | 1 | 7 | 8 |
| -2 | 4 | 29 | 33 |
| Total | 60 | 40 | 100 |

TABLE 4. *Overall accuracy of ramus shape as an indicator of sex in the pathologic African sample*

| Sex | N | Ramus shape scores | | | | Accuracy by sex (%) |
|---------|-----|--------------------|-------|-------------|-------|---------------------------|
| | | -1 & -2 | | 0, +1, & +2 | | |
| | | N | % | N | % | |
| Males | 60 | 5 | 12.2 | 55 | 93.2 | 91.7 |
| Females | 40 | 36 | 87.8 | 4 | 6.8 | 90.0 |
| Total | 100 | 41 | 100.0 | 59 | 100.0 | 91.0 |

scores of 0 through +2 were classified as male, and -1 through -2 as female. The results thus calculated revealed that ramus shape was diagnostic in 99.1% of males and 98.8% of females for an overall prediction accuracy of 99.0% (Table 2).

The same procedure was carried out on the "pathologic" sample (Tables 3 and 4). In general, the results mirrored those of the normative group, including the finding that all scores of 0 were male. The main difference was that classification accuracy dropped to about 93% in males, 88% in females and 91% overall.

The difference between overall accuracies for the two groups was significant ($P < 0.05$). Therefore, the mandibles, skulls, and in some cases postcranial skeletons of misclassified individuals were reexamined. It was observed that most misdiagnosed females had at least one molar missing long enough

TABLE 5. Distribution of ramus shape scores by sex from the American test sample

| Score | Males | Females | Total |
|-------------------|-------|---------|-------|
| Whites (N = 85) | | | |
| +2 | 27 | 1 | 28 |
| +1 | 8 | 0 | 8 |
| 0 | 8 | 2 | 10 |
| -1 | 1 | 4 | 5 |
| -2 | 3 | 31 | 33 |
| Amerinds (N = 66) | | | |
| +2 | 25 | 0 | 25 |
| +1 | 1 | 1 | 2 |
| 0 | 3 | 2 | 5 |
| -1 | 1 | 3 | 4 |
| -2 | 1 | 28 | 29 |
| Blacks (N = 96) | | | |
| +2 | 35 | 1 | 36 |
| +1 | 1 | 1 | 2 |
| 0 | 8 | 3 | 11 |
| -1 | 2 | 8 | 10 |
| -2 | 2 | 35 | 37 |

TABLE 6. Overall accuracy of ramus shape as an indicator of sex in the American test samples¹

| Sex | N | Ramus shape scores | | | | Accuracy by sex (%) |
|----------|----|--------------------|-------|-------------|-------|---------------------------|
| | | -1 & -2 | | 0, +1, & +2 | | |
| | | N | % | N | % | |
| Whites | | | | | | |
| Males | 47 | 4 | 10.3 | 43 | 93.5 | 91.5 |
| Females | 38 | 35 | 89.7 | 3 | 6.5 | 92.1 |
| Total | 85 | 39 | 100.0 | 46 | 100.0 | 91.7 |
| Amerinds | | | | | | |
| Males | 32 | 2 | 6.1 | 30 | 90.9 | 93.8 |
| Females | 34 | 31 | 93.9 | 3 | 9.1 | 91.2 |
| Total | 66 | 33 | 100.0 | 33 | 100.0 | 92.4 |
| Blacks | | | | | | |
| Males | 48 | 4 | 8.5 | 44 | 89.8 | 91.7 |
| Females | 48 | 43 | 91.5 | 5 | 10.2 | 89.6 |
| Total | 96 | 47 | 100.0 | 49 | 100.0 | 90.6 |

¹Ramus shape scores of 0, +1, and +2 were deemed male; -1 and -2, female.

to allow alveolar healing. It was also noted that in one case each of acromegaly and Paget's disease, female mandibles were masculinized. In several cases, leprosy, syphilis, and trauma with indications of healing were linked to deformations that hindered classification in both sexes.

The test samples (including both healthy and pathologic specimens) were examined and scored in the same manner (Tables 5 and 6). In all cases the results were very similar to those of the "pathologic" African sample. For the first time, however, a few females (2 whites, 2 Amerinds, and 3 blacks) had scores of 0. Since 0 is considered male, these were counted as incorrectly sexed. Al-

though the accuracies for these groups were within about 1% of each other and the "pathologic" African sample (ranging from about 91 to 92%), flexure was most pronounced and easiest to observe in Amerinds, followed by blacks. While correctly assessed, as many as 37% of white males were scored +1 or 0, as opposed to 20% of blacks and 13% of Amerinds. Among white males in this study, the flex was more subtle—19% of correctly assessed white males (8/43) had at least 1 indeterminate ramus scored as 0, as opposed to 2% of blacks (1/44), and 3% of Amerinds (1/30), respectively. The tall, thin white ramus was recognizably different from the squarer African and American blacks and robust Amerinds.

White females in this sample often exhibited the gonial prominence with change in direction well below the occlusal plane as in Figure 5B. High flex at the neck of the condyle was rare in all groups. Female rami tended to remain straight, even with as many as 4 molars missing antemortem. Of the total of 3 white females that were incorrectly sexed, only 1 had both rami flexed and the others had 1 side flexed and the other straight (score 0).

Of all samples tested, whites were the only group where females were at least as accurately assessed as males. White males appeared to be most susceptible to remodeling after tooth loss. Tooth loss was relatively minor in the Amerinds—only a few lost more than 2 posterior teeth. In this group, severe dental wear (with as little as 1 or 2 mm of crown remaining) and abscess formation were more common.

Overall accuracy for all mandibles (N = 547) is 94.2% (Table 7). Only the normative African sample at 99% has significantly higher accuracy ($P < 0.05$).

DISCUSSION AND CONCLUSIONS

The results of this study indicate that mandibular ramus flexure has greatly increased the accuracy of sex assessment from the skeleton. In the large normative African sample, ramus shape alone produced 99% correct classification. This surpasses the 95% rate reported from a complete pelvis (Krogman and İşcan, 1986). Genoves (1959)

TABLE 7. Overall sexing accuracy of ramus shape

| | Africans | | Americans | | | Total accuracy |
|--------------|----------|---------|-----------|-------|-------|----------------|
| | Normal | Pathol. | Amerind | White | Black | |
| N (correct) | 198 | 91 | 61 | 78 | 87 | 515 |
| N (total) | 200 | 100 | 66 | 85 | 96 | 547 |
| Accuracy (%) | 99 | 91 | 92.4 | 91.7 | 90.6 | 94.2 |

stated that more optimistic claims for the os coxae should be greeted with skepticism. At 94.2%, overall accuracy from the ramus in all African and American samples combined ($N = 547$) is certainly on a par with the pelvis and superior to the 90% accuracy rate from a complete skull (Krogman and İşcan, 1986). Moreover, a Chi-squared test revealed that diagnostic accuracy from ramus shape was significantly better ($P < 0.01$) than the 75%–85% accuracy reported from the only three published studies (Giles, 1964; Hanihara, 1959; İşcan and Ding, 1995) that quantify sex from the mandible alone.

As is any bone, the mandible is subject to remodeling based on mechanical stress, changes in functional patterns, and disease (e.g., McNamara, 1975; Ortner and Putschar, 1981; Daegling, 1993). The authors noted that leprosy and syphilis may cause significant deformation of the skull and mandible, as can trauma. Paget's disease and acromegaly were linked to enlargement, thickening, and masculinization in females. Tooth loss is also known to alter jaw morphology (see Brace and Mahler, 1971; Daegling, 1993). The authors observed extreme transformations of normal morphological appearance in edentulous mandibles. Yet, the results of this study suggest that the loss of even one molar may result in African females remodeling to either the male ramus shape or an intermediate configuration. Interestingly, the tall thin white male ramus appears to be more susceptible to straightening than the white female is to flexing—even in the edentulous state. Extreme tooth wear appears to be a factor in Amerinds. Informal observations of mandibular variants such as rocker jaw suggest the trait may not be expressed in these cases.

Another consideration is that age at death is not always documented by a birth certificate in these collections. If males thought to be in their early 20s were even just a few

years younger, the development of ramus flexure may not have been complete. Furthermore, substantial postmaturity growth is known to occur in the ramus (Walker and Kowalski, 1975) and elsewhere between the ages of 18 and 27 (e.g., Lubicka, 1944; Hulanicka and Kotlarz, 1983; Roche, 1989). This was particularly noticeable in Terry black males and may have been a factor in Amerinds listed only as "adults." It is also quite possible that there may be sexing errors among the archaeological specimens, because these are unidentified individuals. Despite these potential sources of error, the consistently similar and high accuracy rates in all samples studied—at least 91%—strongly support the validity and the wide ranging applicability of this new trait (Table 7). For additional evidence, we direct the reader to Kennedy et al. (1992) and Milicer (1955). Photographs in these monographs clearly depict both straight and flexed rami in South Asians and Australian Aborigines, respectively. In all cases where ramus shape could be ascertained from the illustrations, sex assessment matched that attributed to the specimen.

As mentioned earlier, mandibular morphology is influenced both by the configuration of the muscles of mastication (e.g., Cwirko-Godycki, 1928; Strzalko, 1970; Malinowski, 1971; Weijs and Hillen, 1986) and changes in cranial shape (e.g., Cheverud and Midkiff, 1992; y'Edynak and İşcan, 1993). Thus, the creation of the flexure is likely to result from a change in the size, strength, or angulation of the muscles of mastication, especially the masseter and medial pterygoid muscles, which attach just below the level of flexure on the ramus. In fact, the authors observed that in males where rugosity of the medial pterygoid muscle attachment is noticeably more pronounced than that of the masseter, the ramus appears much more vertical and the flexure may be



Fig. 6. Mandible of AL-288 (Lucy). This cast (from the Paleoanthropology Research Unit at the University of the Witwatersrand) clearly exhibits a straight posterior margin of the ramus at the level of the occlusal plane, with flexure high at the neck of the condyle (arrow) as in modern females (see Fig. 4) (photo by M. Henneberg).

more subtle or fall into the "indeterminate" category. The temporalis and lateral pterygoid muscles attach well above the flexure. The authors' observations of head dissections revealed that the parotid gland is the only anatomic structure in direct contact with the posterior part of the ramus at the site of flexure. The external carotid artery and its branches, and the inferior alveolar nerve, are normally not in contact with the bone at that point. On the medial aspect of the ramus there is a shallow groove descending from the point of flexure anteroinferiorly into the mandibular foramen. The presence of this heretofore unnamed structure, now designated as the internal posterior groove of the ramus, is responsible for making this area the thinnest portion of the posterior ramus, and, as such, more susceptible to remodeling. This was supported by the authors' observations of two juvenile mandibles with rickets that exhibited bilateral ramus collapse at this site.

The fact that the development of ramus flexure is related to the sexual differentiation of males during puberty is demonstrated

by observations of 80 sub-adult mandibles of both sexes from the Dart collection (Loth, 1996). Both boys and girls have a straight ramus, and flexure is not consistent in males until the end of adolescence. By this time, development of the musculature and its relative strength is disproportionately greater in males (Henneberg et al., 1995), and as mentioned earlier, postmaturity ramus growth continues much longer in males. Furthermore, Enlow and Harris (1964) have shown that final growth takes place in the condylar region, which, as can be seen in their Figure 14, encompasses the triangular region of the flexure. Thus, it appears that ramus flexure is initiated by late growth in males and maintained by optimal muscle balance to preserve the most structurally efficient ramus form. This leads to the conclusion that normal function maintains sex differences and enhances the reliability of this indicator as opposed to many other traits that are rendered equivocal by ordinary usage.

Significantly, the sexually dimorphic ramus shapes reported here are easily observ-

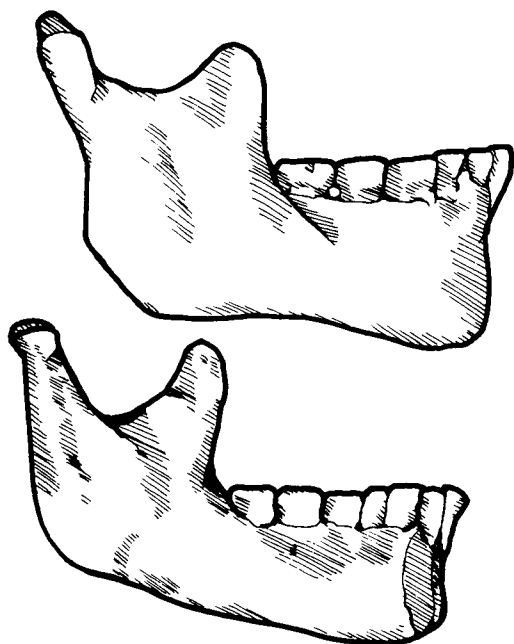


Fig. 7. Sketches of mandibles of Predmost male (above) and female (below). These 26,000-year-old specimens are excellent examples of ramus flexure in the male and straight form in the female.

able in fossil hominids. The authors' preliminary examinations of original fossils and accurate casts (housed at PARU and the Transvaal Museum) have revealed the same, easily discernible, differences in ramus shape in the mandibles of early *Homo sapiens*, Neandertals, *Homo erectus*, and australopithecines (photographic examples can be found in many sources including Wolpoff, 1975, Fig. 7, 20, 23). The mandible of "Lucy" (AL 288), an *Australopithecus afarensis*, is a good example of a straight female ramus with flexure occurring high at the neck of the condyle (Fig. 6). The 26,000-year-old mandibles from Predmost (Fig. 7) are excellent models of the male and female configurations. Further studies are under way to systematically assess this feature on the fossil record. The consistent reliability of ramus shape over time and through paleospecies will greatly enhance our ability to separate sexual dimorphism from evolutionary change. Size and proportions are known to have changed significantly through the ages—even from as recently as the begin-

ning of the Holocene (Henneberg, 1988, 1992). This morphologic trait is not size dependent and can therefore avoid the problems inherent in even the latest metric attempts to diagnose sex and ultimately determine the range of sexual dimorphism in small fossil samples (e.g., Plavcan, 1994).

In conclusion, this study represents the first attempt to quantify the accuracy of assessment of sexual dimorphism from discrete mandibular morphology alone. Although not immediately obvious, the fact that the mandible is at least as dimorphic as the pelvis is not surprising when one considers its growth and development. Differences between the sexes are already significant in utero, continue through childhood, and become further enhanced during and immediately following adolescence. Moreover, in both mammals and primates, dimorphism is pronounced and genetically sex linked (e.g., canine teeth). In all primates, facial appearance and expression are important aspects of reproductive success.

The results of this study support the contention that when a morphologic configuration is clear and consistent this type of sex assessment is superior to the osteometric approach. Obviously, the highest probability of correct diagnosis of sex comes from a complete examination of all bones known to belong to a given individual—no single skeletal indicator should be relied upon exclusively if other proven dimorphic areas are available. The presence or absence of ramus flexure has the potential to be a valuable tool for sexing intact and fragmented mandibles from historic archaeological finds, rare fossil hominids, and modern forensic cases.

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